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Centroceras secundum sp. nov. (Ceramiaceae, Rhodophyta) from the Sultanate of Oman

by

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With 14 figures

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Abstract: Collections of a new species of benthic marine red algae, *Centroceras secundum* M.J. Wynne, were made on the southern coast of the Sultanate of Oman. Plants occurred during the peak of the summertime monsoon on rocky shores subject to maximum wave exposure at elevations ranging upward from the mid-eulittoral into the supralittoral fringe. The species is strikingly separable from other members of the genus *Centroceras* because of the much greater lengths of the thalli, the heavy cortication of the axes, and the secund arrangement of the branching.

Key words: *Centroceras*, *C. secundum*, Ceramiales, marine algae, red algae, Sultanate of Oman, taxonomy.

Introduction

As currently defined, the genus *Centroceras* Kützing contains only five or six species: the lectotype, *C. clavulatum* (C. Agardh in Kunth) Mont. in Durieu de Maisonneuve, along with *C. corallophilloides* R. E. Norris (1993), *C. distichum* Okamura (1934), *C. internitens* Gallagher et Humm (1983), *C. japonicum* Itono (1973), and *C. minutum* Yamada (1944). The previously credited species *C. apiculata* Yamada (1944), *C. bellum* Setch. et N.L. Gardner (1924), and *C. cinnabarinum* (Gratel. ex Bory) J. Agardh (1851) have all been transferred to the genus *Corallophila* by Norris (1993), whereas *Centroceras inerme* Kütz. (1849, 1863) was previously synonymized with *C. clavulatum* by Lawson & John (1982). Giaccone's (1969) *Centroceras pignatii* was also transferred to *Corallophila* by Norris (1993) as a synonym of *Corallophila cinnabarinum*, a judgment supported by Gómez Garreta et al. (2001). Abbott (1999) suggested that *C. corallophiloides* may be conspecific with *C. japonicum* but refrained from formally proposing the synonymization.

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Centroceras clavulatum is a highly variable and ubiquitous species (Hommersand 1963), common in temperate to tropical seas. The other species in the genus, however, have relatively restricted ranges and are only rarely encountered and recorded in the literature. The discovery of a very robust, heavily corticated and distinctively branched new upper eulittoral species of *Centroceras* in the Sultanate of Oman was unexpected, although this region of the world has only recently received close scrutiny and has already been shown to host a rich variety of new and distinct taxa. The large size, well developed cortication and the secund branching of the new species, along with its occurrence from the eulittoral zone to the supralittoral fringe during the monsoon season, all point to its being unlike any other known species in the genus.

Materials and methods

The initial collection of the new species was made in September 2000, with subsequent collections being made in September 2001 during the course of the Algal Biodiversity Project of Oman (1999-2002), a Darwin Initiative grant for the 'Survival of Species'. The specimens were gathered *in situ* from the 'supralittoral fringe'. Material was processed as herbarium mounts soon after collecting. Some specimens were preserved in 5% Formalin/sea-water. Microscope slides were observed on a Zeiss research compound microscope. Some axes were hand-sectioned using a single-edged razor blade. Line-drawings were made with a camera lucida, and photomicrographs were taken with Kodak T-MAX 100 film, were made with a camera-back attached to the same microscope. Habit photographs were taken with a standard 35 mm camera. Field coordinates were obtained by several GPS devices, primarily a Garmin Etrex Summit. Brummitt & Powell (1992) have been followed in regard to the authors of plant names, and herbarium abbreviations are according to Holmgren et al. (1990).

Results

DIAGNOSIS: *Centroceras secundum* sp. nov. Aliis speciebus in genere multum robustiore statura thallorum, usque ad 60 cm alt., distincta; thalli multo ramosi, fusco-rubro-brunnei in stato optimo; axes primarii percurrentes, ramos distichos, alternantes laterales ferentes, qui ordinatio horum ramorum reflexorum repetant; numerosi ramosi breves determinati in pagina adaxiali rami densiter et unilateraliter producti; haec ramificatio densa aspectum velutinum thallis textura coacta aut spongiosa faciens; 8-11 cellulae periaxiales per nodam productae; cellulae filamentorum primariorum corticalium divisiones periclinales subeuntes, corticationem plus producentens, et cellulae derivatae earum divisiones periclinales continue subeuntes corticationem incrassatam in axibus vetioribus formantes; spinae in pagina exteriore ramorum juniorum plerumque adsunt, in pagina interiore reductae aut saepe absunt; cellulae glandulae absunt; cystocarpia terminaliter in ramis brevibus producta, 6-10 ramis involucralibus subtentis superata.

Centroceras secundum differs from other species in the genus by the much more robust stature of the thalli, up to 60 cm in height; the thalli are much branched and dark reddish-brown in the optimal condition; the primary axes are percurrent, distichously branched, bearing alternating lateral branches that bear further orders of alternate-distichously arranged laterals that are reflexed or curved downward; numerous short determinate branches are densely and unilaterally produced on the adaxial surface of the parent branch; this dense ramification results in a felt-like or spongy appearance; 8-11 periaxial cells produced per node; the cells of the primary cortical filaments undergo periclinal divisions to produce additional cortication, and

their derivatives continue to undergo periclinal divisions to develop massive cortication in older axes; spines are often present on the outer side of the younger branches but are often absent or reduced on the inner side; gland cells are absent; cystocarps are produced terminally on short branches and are subtended by 6-10 arching involucral branches.

HOLOTYPE: Western side of Wadi Zeid (Hoon's Bay) (16.944967°N, 54.80402°E), east of Mirbat, Dhofar, Sultanate of Oman: 9.ix.2001, leg. M. Wynne 09092001-04-12; cystocarpic; deposited in MICH.

ISOTYPES: deposited in BM, GENT, ON, PC.

Additional collections (all from Oman):

Type locality: 17.ix.2001, leg. M. Wynne 17092001-12-05, cystocarpic (BM, MICH, ON). Kah'f Al Marnaif, Al Mughsayl (16.87575 N, 53.76676 E), Dhofar: 15.ix.2000, leg. M. Wynne 15092000-08-15, cystocarpic (BM, MICH, ON); 11.ix.2001, leg. M. Wynne 11092001-11-09, cystocarpic (BM, MELU, MICH, ON, SAP and US). Raaha (= Alto) Bay (16.95116°N, 54.81650°E), east of Wadi Zeid and east of Mirbat, Dhofar: 12.ix.2001, leg. M. Wynne 12092001-07-34, cystocarpic (MICH, ON).

VEGETATIVE STRUCTURE: Main axes are robust, erect, to 60 cm tall (Fig. 1), much branched, and dark reddish-brown, becoming orange-yellow when sun-bleached or late in the growing season; attachment is by a rhizoidal discoid mass; main axes reach 5 mm in thickness near base; primary axes tend to be percurrent and bear distichously arranged alternating lateral branches, the first order of laterals bearing further orders of alternate-distichously arranged laterals that are reflexed or curved downward (Fig. 1); numerous short determinate branches are densely and unilaterally produced on the adaxial surfaces of all the indeterminate branches (Fig 2, 4), giving the thalli a felt-like or spongy texture; periaxial cells number 8-11 per node (Figs 7-9); spines are present mostly on the abaxial side of axes (Figs 3, 5), although not always because in some they are produced bilaterally on in whorls (Fig. 6); gland cells absent.

Examination of axes in close proximity to the apex showed that there are two descending cortical filaments associated with each periaxial cell, thus a total of 16-22 in total. Each periaxial cell cuts off three cells (Figs 10-12). The first one is cut off distally. It cuts off two cortical cells distally, one of which may produce a spine (Fig. 12). A second distal is cell cut off from the periaxial cell, and from it usually a single distal cell is produced as well as a basipetal corticating filament (Figs 10, 11). A third cell cut off from the periaxial cell gives rise directly to a basipetal corticating filament. Within 6 or 7 segments from the apex, it can be observed that the cells making up the corticating filaments undergo periclinal divisions, cutting off cells to the outside (Fig. 12). Spine cells may also be formed by these corticating cells, as detected by the refractive nature of the potential spine cells. Continued periclinal divisions of the cells of the corticating filaments and their derivatives contribute to the eventual massive cortication covering the mature axes. This cortication does not have a rhizoidal appearance but a pseudoparenchymatous aspect.

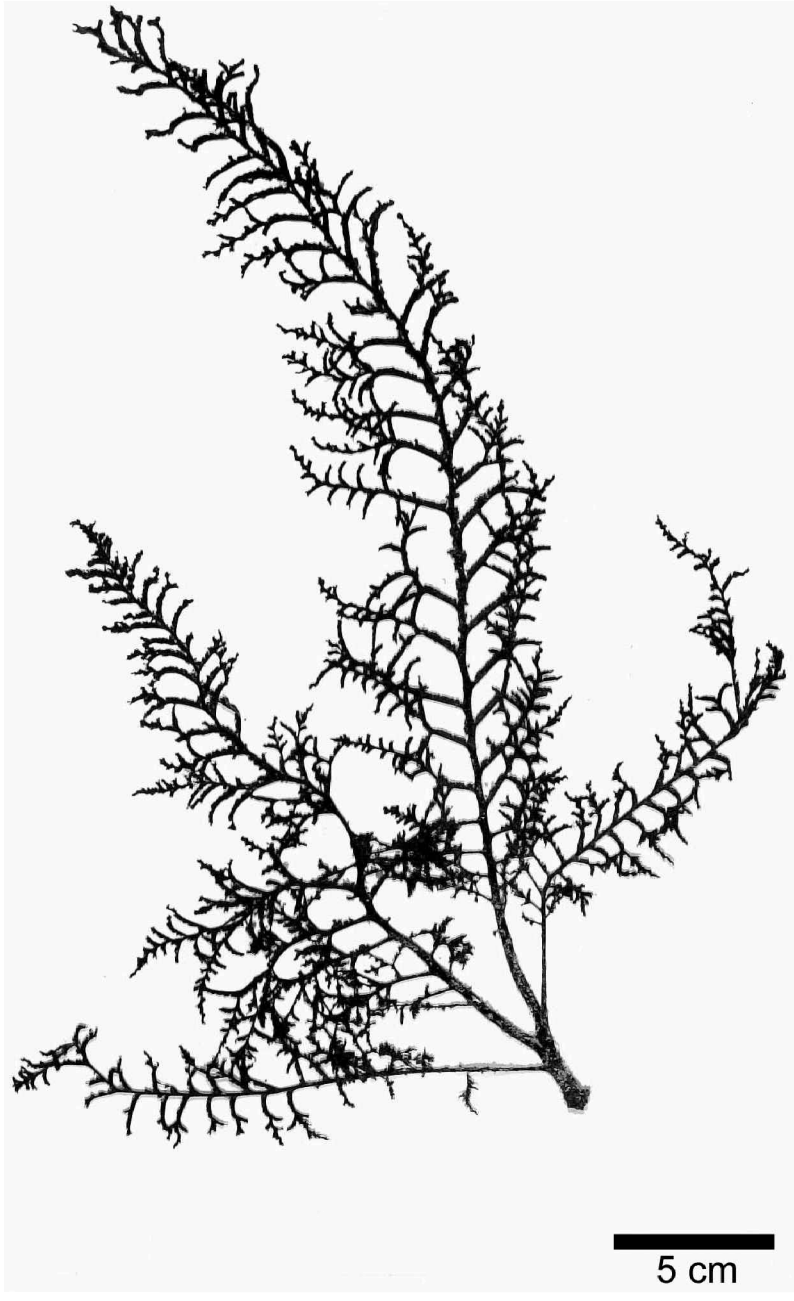
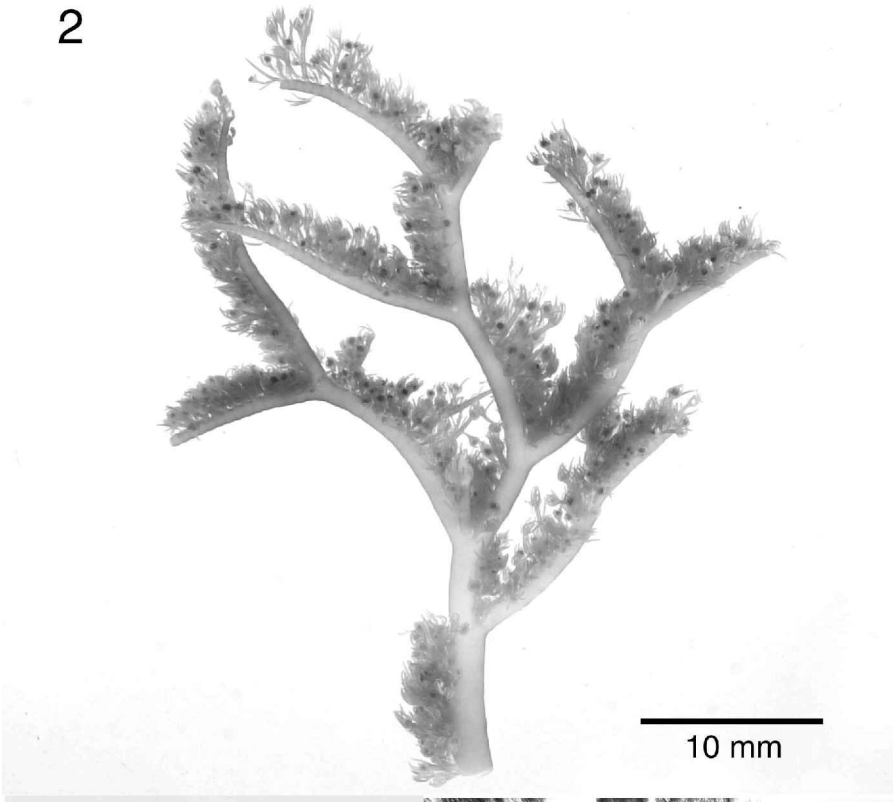


Fig. 1. *Centroceras secundum* M.J. Wynne sp. nov. Holotype specimen (MICH).

Figs 2-4. *Centroceras secundum* M.J. Wynne sp. nov. Vegetative features. Fig. 2. Portion of thallus with secundly arranged branches. [2001-12-05]. Fig. 3. Young axis bearing spines. Fig. 4. Cross-section of older axis bearing adaxial branches.


2
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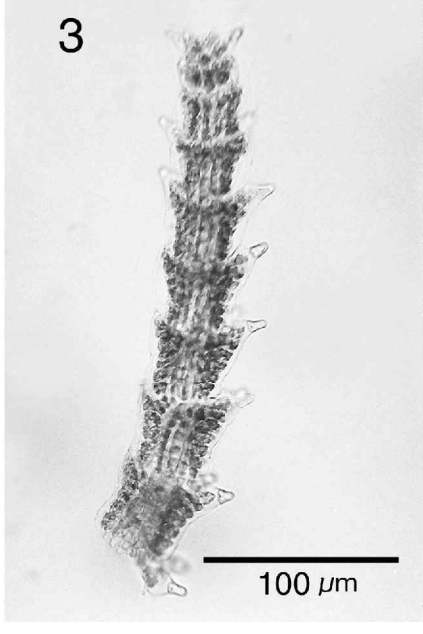
3
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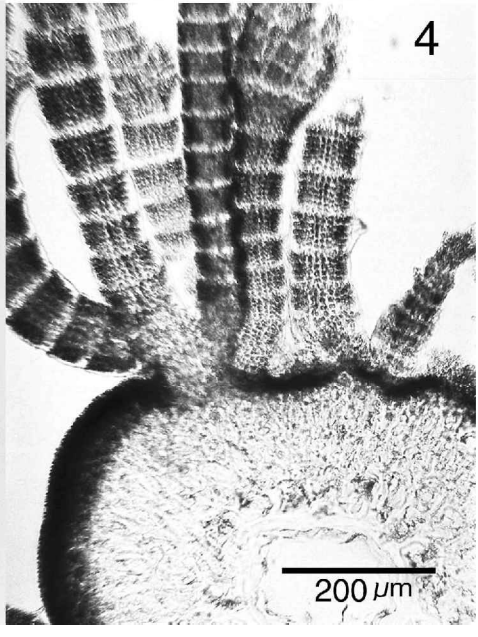
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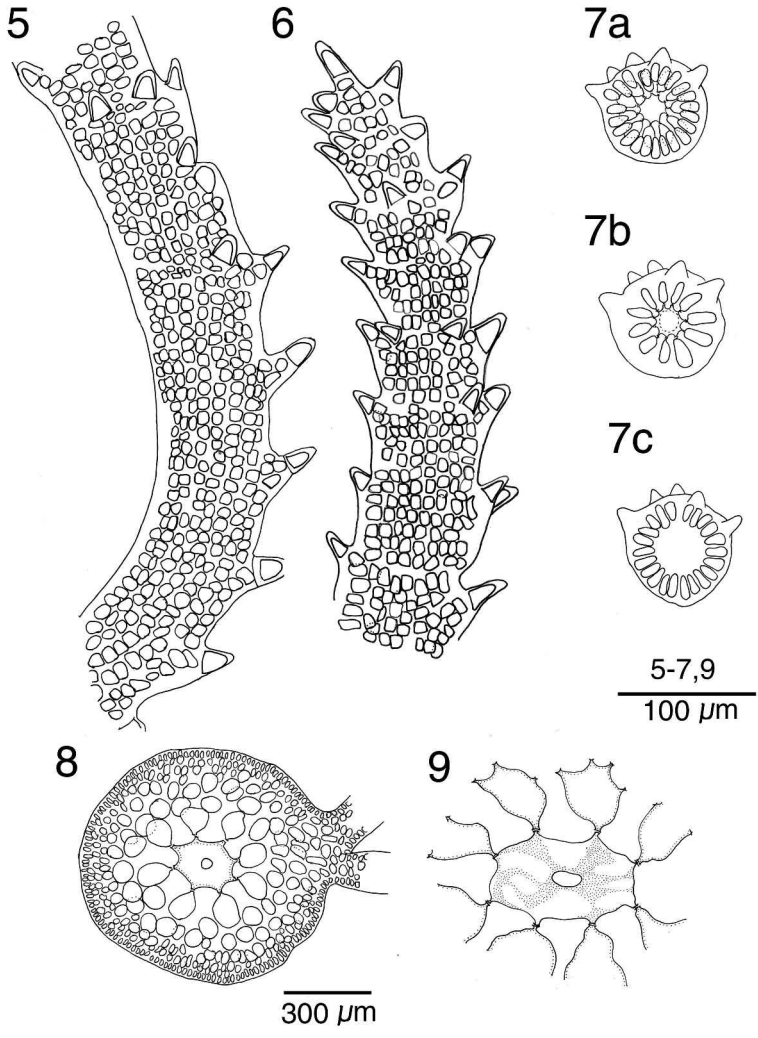
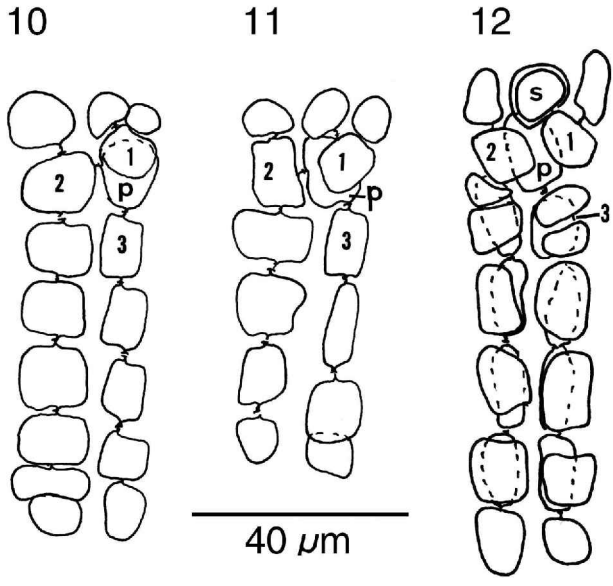


Figs 5-9. *Centroceras secundum* M.J. Wynne sp. nov. Vegetative features. Camera-lucida drawings. Figs 5 & 6. Young axes bearing spines and displaying primary cortication. Fig. 7. Cross-section of young axis at nodal region showing 11 (inner) periaxial cells and 22 (outer) cortical cells (7a), schematic view showing only the periaxial cells (7b), and schematic view showing only the cortical cells (7c). Fig. 8. Cross-section at a node with eight periaxial cells, 6-7 layers of secondary cortication, and the bases of two determinate laterals. Fig. 9. Detail of a central-axial cell pit-connected to eight periaxial cells.

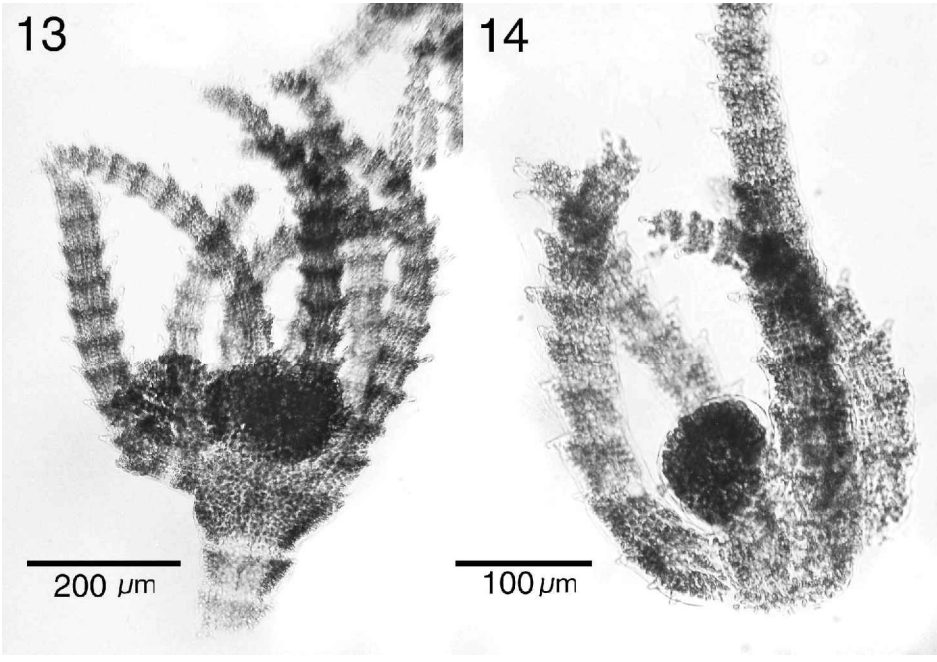
REPRODUCTION: Only female gametophytes with cystocarps were observed. The latter are produced at the ends of foreshortened indeterminate branches, as their initiation appears to cause cessation of growth of the bearing axis. Mature cystocarps are



Figs 10-12. *Centroceras secundum* M.J. Wynne sp. nov. Formation of basipetal corticating filaments. Each periaxial cell (*p*) cuts off three cells, two of them distally (*1*, *2*) and one proximally (*3*). Cell 3 produces a corticating filament directly, and cell 2 cuts off two cells, the proximal one forming the second corticating filament. Fig. 12. Early stage of cortication resulting from periclinal division of the primary cell layer; spine cell (*s*) also present. Camera-lucida drawings. (*p*, periaxial cell; *s*, spine cell; *1*, *2*, *3*, first, second, and third cells cut off by periaxial cell.)

subtended by 6-10 dwarf branches that laxly invest and arch around the carposporophyte (Figs 13, 14). Carposporophytes are globose to ovoid, 280-360 μm in greatest dimension, and usually contain a single mass of carposporangia but may consist of up to three sequentially produced and synchronously maturing gonimolobes. Carposporangia are spherical and (16-) 20-28 μm in diameter.

HABITAT: Thalli grew as scattered individuals attached to rocky substrata in the very exposed mid-littoral into the 'supralittoral fringe' (Stephenson & Stephenson 1972) in association with *Melanothamnus somalensis* Bornet & Falkenb. (Wynne & Banaimoon 1990), which formed a dense dark purple-blackish band of approx. 3 meters vertical extent. A bright green band of *Ulva fasciata* Delile extends even higher into the supralittoral fringe, above the band of *Melanothamnus*. Most of the *Centroceras* specimens were hand-picked from a sloping platform right above a sheer vertical rock cliff. Because of the fact that this purplish-black band made up mostly of *Melanothamnus* and also the intermingling *Centroceras* ranges from the supralittoral fringe downward into the mid-eulittoral zone, it is assumed that *C. secundum* extends into the eulittoral. The dangerous conditions precluded any collecting in the littoral zone. During the summertime monsoon season, which starts in May and ends in September, this dark band of algal growth extends well above the high-



Figs 13 & 14. *Centroceras secundum* M.J. Wynne sp. nov. Cystocarp morphology. Multiple- (Fig. 13) and single-lobed (Fig. 14) carposporophytes surrounded by involucral branches.

tide mark because of the constant buffeting of waves of extremely high energy (Savidge et al. 1990). The sites where *C. secundum* has been collected can all be characterized as having full exposure to the waves. The monsoon-driven system brings relatively cold, nutrient-rich water from great depths due to the upwelling (Currie et al. 1973, Sheppard et al. 1992). The rich eulittoral and supralittoral flora so characteristic of the monsoon system on this shoreline essentially disappears during the non-monsoon season.

Discussion

Centroceras secundum differs substantially from the other members of the genus. The lengths of its thalli, which can be up to 60 cm, are at least three times greater than those previously recorded for any other species, most of which range from < 1 to at most 10-20 cm in length (Norris 1993, Abbott 1999). Thallli of *C. internitens* are up to 5 cm tall (Gallagher & Humm 1983). Thalli in *C. distichum* tend to be creeping, decumbent, or prostrate (Tanaka 1950, Itono 1977, Boo & Lee 1985, Stegenga et al. 1997). The only species of *Centroceras* that reaches a possible height of 10-20 cm is *C. clavulatum* (Taylor 1960, Stegenga et al. 1997, Womersley 1998,

Littler & Litttler 2000), but it is usually only about 4-5 cm in height (Boo & Lee 1985, Abbott 1999).

All other species of *Centroceras* have axial cells completely covered between the nodes with a single layer of cortication consisting of longitudinal rows of regularly aligned subrectangular cells, and the cortication is restricted to that level of development. In *C. secundum*, however, this initial layer of cortication is completely covered by extensive further layers of cortication, resulting in thickly corticated axes. Thus, it is only in the young tips (Figs 5, 6) that *C. secundum* shows a strong resemblance to *C. clavulatum* and other *Centroceras* species. The regularly arranged, longitudinal series of cortical cells characteristic of *Centroceras* are readily apparent, and the projecting spine cells arising at the nodes, as in most other species of the genus, are also evident. The subsequent development of extensive additional cortication soon covers up the initial cortical layer.

Another distinctive feature of the new species is the secund nature of the branching (Figs 1 & 2). The primary axes tend to be percurrent and bear alternate-distichous laterals. These lateral branches show a unilateral branching pattern, the branches typically reflexed and arching. Once these secondary laterals have become heavily corticated, numerous smaller branches arise from one side of their surface (Fig. 2). It is not a single small branch that arises from a given region but numerous branches arise side by side, giving a tufted appearance all along the bearing side of the parent branch. No other *Centroceras* species displays this distinctive branch pattern.

The 8 to 11 periaxial cells per node present in *Centroceras secundum* is less than the 10-14 cells in *C. clavulatum* and the 16-20 in *C. internitens* (Gallagher & Humm 1983). According to Norris (1993) there are 6-8 periaxial cells per node in *C. corallophiloides*, whereas there are 10-12 such cells per node in *C. distichum* (Itono 1977). The 8-11 periaxial cells per node of *C. secundum* are at the lower end of the spectrum but are otherwise typical of the genus.

In recent years several authors have attempted to refine generic distinctions among members of the tribe Ceramieae, i.e., those members of the family Ceramiaceae in which axes become partially or totally covered with acropetal, basipetal or both acropetal and basipetal corticating filaments (Hommersand 1957, Ardré 1987, Norris 1993, Boo & Lee 1994). As a result of these efforts, the circumscriptions of the genera *Ceramium* Grev., *Centroceras* Kütz., and *Corallophila* Weber van Bosse (including *Ceramiella* Børgesen) have come to be based on criteria such as the number of corticating cells or filaments per node and their direction of growth (basipetal or acropetal, or both), the shape and the arrangement of the internodal cortical cells, the presence of absence of inner cortical cells, and the position of the tetrasporangia (exserted or immersed) (Cho et al. 2000). The genus *Centroceras* has come to be restricted to species in which the basipetal filaments originate from two locations: a) directly from each periaxial cell, and b) from a basal acropetal cell derived from each periaxial cell, two basipetal filaments thus forming, one directly and one indirectly, from any given periaxial cell (Norris 1993). This is in contrast to the superficially similar *Corallophila*, in which two basipetal filaments are formed directly on each periaxial cell (Norris 1993). The observations of the development of the

corticating filaments in *C. secundum*, as described in the 'Results', confirm its assignment to *Centroceras*.

The new species joins several which have also been reported from the Indian Ocean (Silva et al. 1996), including the type species, *C. clavulatum*, the probably synonymous *C. cryptacanthum* Kützing var. *longiarticulatum* Kützing (Silva et al. 1996, p. 389), and two species, *C. minutum* Yamada and *C. distichum* Okamura, originally described from Japan. *Centroceras minutum* was reported from the Maldives (Wynne 1993) and the Seychelles (Wynne 1995), whereas *C. distichum* is now known from South Africa (Jackelman et al. 1991, Stegenga et al. 1997). Only *C. clavulatum* has previously been recorded from Oman and other localities in the Arabian Sea.

The benthic marine algal flora of the Dhofar region of the Sultanate of Oman continues to demonstrate a wealth of new records and new taxa (Nizamuddin & Campbell 1995, Wynne 1998, 1999a, 1999b, 2000, 2001a, 2001b, 2002a, 2002b, 2003, Wynne & de Jong 2002, Wynne & Jupp 1998, Wynne & Leliaert 2001, Schils & Coppejans 2002, Schils et al. 2003), to which *Centroceras secundum* can now be added. Particularly noteworthy about the new species are its eulittoral to supralittoral, high-energy habitat and restricted monsoonal growing season, features that, along with its unique size and construction, serve to establish it as the most distinctive member of the genus *Centroceras*. Unresolved question about the new species include why all the specimens collected were cystocarpic and how and where it survives during the non-monsoon period.

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